

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Papers in Behavior and Biological Sciences

Papers in the Biological Sciences

1996

Predicting Cognitive Capacity from Natural History: Examples from Four Species of Corvids

Russell P. Balda

Northern Arizona University,, Russell.Balda@nau.edu

Alan Kamil

University of Nebraska - Lincoln, akamil1@unl.edu

Peter A. Bednekoff

University of British Columbia

Follow this and additional works at: <https://digitalcommons.unl.edu/bioscibehavior>



Part of the [Behavior and Ethology Commons](#)

Balda, Russell P.; Kamil, Alan; and Bednekoff, Peter A., "Predicting Cognitive Capacity from Natural History: Examples from Four Species of Corvids" (1996). *Papers in Behavior and Biological Sciences*. 15.

<https://digitalcommons.unl.edu/bioscibehavior/15>

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Behavior and Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Published in *Current Ornithology*, Volume 13, edited by V. Nolan Jr. and E. D. Ketterson. Plenum Press, New York, 1996, pp. 33–66. Copyright © 1996 Plenum Press, New York. Used by permission.

Predicting Cognitive Capacity from Natural History:

Examples from Four Species of Corvids

Russell P. Balda

Department of Biological Sciences, Northern Arizona University,
Flagstaff, Arizona 86011

Alan C. Kamil

School of Biological Sciences, University of Nebraska–Lincoln,
Lincoln, Nebraska 68588

Peter A. Bednekoff

Department of Biological Sciences, Northern Arizona University,
Flagstaff, Arizona 86011 (*Present address* — Institute of Applied Mathematics
and Centre for Biodiversity Research, University of British Columbia,
Vancouver, British Columbia, Canada V6T 1Z2)

1. Introduction

Birds have been studied for centuries because they are numerous, conspicuous, and aesthetically pleasing to humans. Despite their overall regard for birds, historically, many ornithologists have considered birds as instinct-driven organisms of little intellectual capacity. For example, the ornithological textbook of choice from the 1960s states the following view of avian intelligence:

Flight has proven to be an enormously successful evolutionary venture, but one that has cost birds dearly in mental development. In effect,

flight has become a substitute for cleverness; birds solve many potential problems merely by flying away from them. ... As a consequence, much [avian] behavior is, by mammalian standards, fragmentary, stereotyped, and at times amazingly stupid. (Welty, 1962, p. 159).

Research over the past 30 years has shown that this view of birds is incorrect. Field studies have demonstrated that birds possess considerable behavioral adaptability, often engaging in flexible and opportunistic behaviors while foraging, communicating, selecting mates, interacting in social groups, and avoiding predators (see Krebs and Davies, 1984). Laboratory studies have demonstrated that birds perform very well in solving a variety of complex cognitive problems (e.g., Pepperberg, 1990; Vaughan, 1988; Herrnstein, 1985; Kamil et al., 1977). Interestingly, the ability to solve many of these complex problems was once thought to be the exclusive province of primates. As Marler has suggested (this volume), the intellectual abilities of birds in some areas may be broadly equivalent or superior to that of mammals. Thus, understanding cognitive abilities of birds is an important issue for ornithologists. Most previous work on cognition in animals has been carried out by experimental psychologists who have not carefully considered either the ecological setting or evolutionary history of their subject species (see Kamil, 1988a). In this paper we present an explicit evolutionary approach to the study of cognition, with an emphasis on the use of comparative studies. Although this approach is quite general, it is particularly appropriate for ornithological studies.

2. General Problems and Approach

A central problem confronting all organisms is the capture and utilization of resources. Much biological research has focused on how this occurs. Historically, attention was given first to relatively obvious factors, such as physical characteristics and fighting ability. However, as our understanding of how animals gain control of resources has increased, we have gradually come to appreciate the roles of relatively subtle factors, such as signals and communication (Spector, 1992). Our approach begins with the observation that the acquisition and use of knowledge contributes importantly to the ability of animals to gain essential resources. The primary implication of this position is that the mechanisms animals use to gain knowledge about their environments are adaptive traits. Therefore, the methods developed for the study of adaptation can be applied to these traits (e. g., Williams, 1966).

Various studies have demonstrated that animals use information about their environment (knowledge) adaptively. Two of the most im-

portant arenas for the adaptive use of cognitive abilities are obtaining food and interacting with other animals. The importance of cognitive abilities is implicit in many optimal foraging models. In general, these models show that animals can substantially increase their foraging efficiency by reacting facultatively to various parameters of the distribution of their food. In many cases, this facultative behavioral change is mediated by cognitive processes, particularly learning and memory (e.g., Shettleworth, 1984, 1993; Kamil and Yoerg, 1982; Pulliam, 1981, 1980). For example, in situations where multiple prey types are available, the optimal diet is a function of the relative values and availabilities of the prey types (MacArthur and Pianka, 1966). Therefore, in order to maximize foraging efficiency, the animal needs to know the relative value and availability of the types. Both of these can be learned. Pulliam (1981) demonstrated that Chipping Sparrows (*Spizella passerina*) learn the relative values of seeds that differ in handling time. Also, many studies have demonstrated that animals adjust their diet choices as prey availability changes, in both field (e.g., Goss-Custard, 1981) and laboratory (e.g., Krebs et al., 1977) settings, indicating the importance of learning.

Particularly impressive demonstrations of the adaptive use of learning come from studies that show that 'sampling behavior' varies as a function of environmental parameters (e.g., Krebs et al., 1978). Lima (1984) set up a situation in which Downy Woodpeckers (*Picoides pubescens*) had to explore patches to determine which contained food. In order to make this determination, the birds had to sample the patches. It is this sampling behavior that allows the birds to learn the value of the current patches. Lima found that the woodpeckers adjusted their sampling behavior adaptively as a function of environmental parameters. They sampled patches with no food less frequently when the no-food patches were of high density than when they were of low density. This makes sense because high-density patches are easier to detect as a group than low-density patches. By showing that easier problems are more readily solved than difficult ones, Lima demonstrated the woodpeckers' ability to adjust its sampling dynamically.

There are also many examples of learning and cognition in social settings. Two of the best known examples are imprinting and song learning, but there are many examples with subtle effects as well. For example, it is well known that animals can learn to distinguish the songs of neighbors from the songs of non-neighbors (e.g., Falls, 1992; Myrberg and Riggio, 1985). This knowledge about the songs of neighbors can result in a potentially more efficient territorial defense (Stoddard, 1997; Beecher et al., 1994; Staicer, 1991). The animal can avoid entering energetically expensive contests with neighbors with which it shares well-established terri-

torial boundaries. But, if the individually recognized song comes from a wrong location, then a very energetic response may result (see Falls, 1992, for a collection of references).

Another example of cognition in a social setting comes from studies of the Dunnock (*Prunella modularis*). Based on knowledge of fine-scale differences in territory quality and sex ratio, Dunnocks adjust their social system, adopting monogamy, polygyny, or polyandry when each would seem advantageous (Davies, 1992). These results imply that individual Dunnocks adjust their social behavior depending on an active assessment of several social and nonsocial environmental parameters.

While it is clear that using information about the environment to guide behavior can have large effects on biological success (fitness), how do birds come to have such knowledge? To acquire such knowledge, an animal needs to have had access to appropriate experiences and to possess the cognitive mechanisms necessary to transform these experiences into knowledge that can then be used. The learning mechanisms that allow animals to alter their behavior based on experience are traits that may vary within and among species. Variation in the ability to acquire, store, and use information about the environment can be shaped by natural selection.

In recent years, psychologists have changed the way they conceptualize learning in animals. For many years, the dominant view of animal learning among psychologists emphasized processes of associative learning (Pavlovian, or classical, conditioning) and reinforcement (operant conditioning) while the animal was conceptualized as being passive. In recent years, however, psychologists interested in animal learning have come to emphasize a cognitive approach (e.g., Roitblat et al., 1984), which views organisms as more active, dynamically acquiring, encoding, storing, recalling, and using information (see Anderson, 1990). These stages of information processing are basic components of cognition. Consequently, there is surprising agreement in the basic view of animal learning emerging from laboratory studies by psychologists, and field studies by biologists, especially behavioral ecologists (Real, 1991). These trends increase the chances of constructive integration of laboratory and field approaches to understanding animal cognition.

3. The Study Of Cognitive Adaptations

The central theme of this chapter is that cognition is part of the adaptive arsenal with which animals cope with environmental demands. If this

is correct, then information processing abilities will need to be understood as adaptive traits that are the result of the same evolutionary processes that are known to affect morphological traits. This means that the methodology developed for the study of the adaptive function of physical traits should be applied to the study of cognitive traits. The most widely used methods include the correlation of naturally occurring individual variation with biological success, the use of direct experimental intervention to create variation, and the comparative method.

If a trait is adaptive, then individuals who vary in that trait should have varying biological success. Thus, the adaptive approach predicts correlations between trait value and fitness. An elegant example of such research is that of Endler (1980), demonstrating that variation in male coloration in guppies (*Poecilia reticulata*) is correlated with mating success. Another example, in this case involving foraging efficiency, is that of Morse and Fritz (1987), who demonstrated that foraging efficiency is a measure of the fitness of foraging crab spiders (*Misumena vatia*). The correlational approach will be difficult to apply to the study of cognitive abilities because these abilities are not directly observable. In order to measure the cognitive ability of an animal, the responses of that animal to environmental change must be studied systematically. Therefore, the correlational approach will require a system in which a biologically relevant cognitive ability can be quickly measured, ideally in the field. For example, might individual variation in the response to neighbor song playback experiments (Beecher et al., 1994; Weary and Krebs, 1992) correlate with some measure of biological success? Might individual variation in the ability to discriminate prey quality affect whether diet selection is optimal and thus affect fitness in Blue Jays (*Cyanocitta cristata*) (Yoerg and Kamil, 1988)?

Relating experimentally manipulated traits to fitness is a particularly powerful method—one that has been applied to a wide variety of traits, including nest location within a colony (Tinbergen et al., 1967), clutch size (Pettifor et al., 1988), tail length (Andersson, 1982), number of helpers at the nest (Brown and Brown, 1981), and suites of hormonally mediated traits (Ketterson et al. 1996). This approach has a number of advantages over the strictly correlational approach. Two are particularly important. First, experimental manipulation allows animals to be assigned to conditions randomly, controlling for factors that might mask a relationship between cognition and fitness. Second, as a practical matter, many biologically important traits show little variation, and experimental manipulation is needed to produce subjects whose fitness will be more variable than that of individuals within the natural population (e.g., Tinber-

gen's 1963 studies of egg coloration). There are two ways to use direct experimental manipulation to study cognitive traits. In the first, different animals can be given different experiences. For example, Hollis (1984) provided a group of male paradise fish with a cue that predicted the appearance of another male (from behind a barrier), while other males did not receive this experience. When two males, one from each group, were placed on either side of an opaque barrier, the predictive cue turned on, and the barrier lifted, the fish for which the cue was informative invariably won the ensuing encounter. This demonstrates the value of information. Furthermore, if the control fish are thought of as representative of fish that lack the ability to learn the meaning of a predictive cue, these data can be taken to demonstrate the adaptive significance of the ability to learn. Similar evidence is provided by studies demonstrating that male songbirds that have had the opportunity to learn appropriate song are more attractive to females than males that have been deprived of that opportunity (McDonald, 1989; Catchpole, 1986; Catchpole et al., 1986).

In the second experimental approach, cognitive ability can be directly manipulated through lesions of the nervous system or by blocking sensory channels. For example, deafened birds of some species do not learn the appropriate adult song (Konishi and Nottebohm, 1969). Black-capped Chickadees (*Parus atricapillus*) (Sherry and Vaccarino, 1989) and Eurasian Nutcrackers (*Nucifraga caryocatactes*), (Krushinskaya, 1966) with hippocampal lesions lose the ability to accurately recover food they have cached. To date, studies of this type suffer from two shortcomings. Although they suggest a direct link between cognitive ability and biological success, studies that directly measure the impact of manipulation of cognitive ability on reproductive success remain to be done. In addition, most current methods for directly interfering with a cognitive ability are relatively crude. In the near future, advances in neuroscience are likely to offer finer methods for imaging, tracing, stimulating, and disrupting brain functions.

The comparative method for studying adaptation, choosing species to compare based on their phylogeny and ecology, is the classic method. This method is again receiving a great deal of attention (e.g., Brooks and McLennan, 1991; Harvey and Pagel, 1991). It has been applied to a wide variety of traits, such as courtship behavior in Anatidae (Lorenz, 1941), beak morphology in Darwin's finches (Grant and Grant, 1989; Lack, 1947), parental and nestling behavior in gulls and terns (Tinbergen, 1960), the socioecology of finches (Crook, 1965, 19641, and mating preferences in poeciliid fishes (Basolo, 1990). The comparative approach can clearly be applied to the study of cognitive processes. Just as wing shape

in swallows and foot structure in ducks reflect adaptations to ecological situations, cognitive abilities should also reflect ecological requirements. If cognitive abilities are adaptive traits, they will vary quantitatively and/or qualitatively in response to differing ecological demands, as do morphological and physiological traits (Shettleworth, 1993; Kamil, 1988a). Later in this chapter, we will present examples of how specific testable hypotheses about cognitive abilities can be generated from knowledge of ecological situations.

Each of the methods discussed above has particular strengths and weaknesses. Therefore, appropriate application of any of these methods to cognition will require special attention to the hypotheses selected for testing and the experimental designs used. Furthermore, cognitive processes are more difficult to measure than physical or simple behavioral traits. Gathering appropriate data will be challenging. Because of these difficulties, data for broad statistical comparisons (see Harvey and Pagel, 1991) will generally not be available. Comparative studies of cognition will generally focus on a few well chosen taxa. The remainder of this chapter will concentrate on the challenges of applying the comparative method to the study of cognitive processes.

4. The Comparative Study Of Cognition

In general, species differences can be understood in terms of two types of causation: phylogenetic and ecological. However, species never share identical phylogenies or ecologies. Therefore, multiple comparisons among species will provide a robust approach to understanding whether similarities and differences are due to common history or common ecology. Support for hypotheses about adaptations can come from the study of two processes, divergence and convergence. Divergence leads to differences that correlate with ecological differences among closely related species. Convergence leads to similarities among distantly related species with similar ecologies. The strongest support for adaptation is found when comparisons of two or more distantly related groups of animals yield similar patterns of divergence within the groups, and convergence between the groups (Harvey and Pagel, 1991).

The comparative study of cognition begins with the study of animals in their natural settings. The thrust of these studies will combine basic descriptions of a species' natural history with detailed recordings of specific behaviors of individuals observed over time. Given these two types of information, hypotheses can be formulated about the function of a given

behavior and the potential role of cognitive mechanisms in its use. Next, to establish whether the behavior requires cognition, laboratory and/or field experiments must be designed that capture the essence of the relevant ecological situation while adding the element of control. Once such studies have established the existence of ecologically relevant cognitive abilities in a single species, an effort that can be valuable in its own right, comparative study is possible.

Species to be compared can be selected on the basis of the extent to which they face a common problem in nature. Closely related species that differ in the frequency with which they face the problem can be studied for evidence of divergence, while distantly related species that face the same problem can be studied for evidence of convergence. Experiments must tap the relevant cognitive process in a meaningful way. Only when species have been shown to differ in a similar pattern in several different tests of the same general capacity can we be confident that the species differ in that capacity (Kamil, 1988a). Furthermore, experimental design often involves a trade-off between ecological complexity and relevance on the one hand, and internal consistency and rigorous controls on the other (Kamil, 1988b). Therefore, parallel results obtained from a series of experiments designed along this trade-off gradient of realism versus control provide powerful support for both the existence of these cognitive abilities and their ecological relevance.

Finally, support for general hypotheses about the adaptive function of cognitive traits will require replication with different taxa. In order to apply this approach, we need detailed natural history information about the species to be tested. Perhaps more is known about the ecology and behavior of birds than any other taxon. There is also a great deal of diversity in many aspects of their behavioral ecology, from social systems to foraging specializations. This is one of the reasons we believe that ornithologists are particularly well-positioned to make a major contribution to the comparative study of cognition.

4.1. *Three Examples from Corvids*

Our approach is similar to Shettleworth's (1993) "ecological program" for comparative psychology. We illustrate this paradigm with three examples from our own research on four seed caching corvids: Clark's Nutcrackers (*Nucifraga columbiana*), Pinyon Jays (*Gymnorhinus cyanocephalus*), Scrub Jays (*Aphelocoma coerulescens*), and Mexican Jays (*Aphelocoma ultramarina*). The first example, that of species differences in spatial memory correlated with dependence on stored food, is one that we have been test-

ing for over a decade. The results of this research program demonstrate the utility of this approach. The second and third examples, centering on sex differences in behavior and species differences in social learning, are in much earlier stages of development and are more hypothetical.

4.2. Environmental Conditions

We selected these four species for study because they experience different climatic conditions due to their elevational distribution, which has led to differential dependence on previously cached food for winter survival and reproduction. These four species cache conifer seeds each fall when the cone crop ripens. Pinyon pines (*Pinus edulis*, *P. monophylla*) are the most commonly cached species in our study area in north-central Arizona, but limber pine (*Pinus flexilis*), ponderosa pine (*Pinus ponderosa*), Mexican pinyon (*Pinus cembroides*), and whitebark pine (*Pinus alba-caulis*) are also commonly harvested in other areas within the distributional range of these birds. Seeds and cones of the pinyon pine have a suite of adaptations that increases corvid harvesting efficiency and thus promotes seed caching behavior (Benkman et al. 1984; Vander Wall and Balda, 1981,1977).

Clark’s Nutcrackers are permanent residents of the mixed coniferous forest at elevations of from 2200 to 3200 m in the mountainous western United States, where they experience harsh winters with low temperatures, cloudy skies, and deep snow (Table I, column 2). Primary and secondary productivity during the winter is nil, and these birds must depend upon hidden food stores for between 80 and 100 percent of their winter diet (Giuntoli and Mewaldt, 1978). Nutcrackers breed in late winter and very early spring and feed their nestlings pine seeds (Mewaldt, 1956).

Table I. Predictions of Cognitive Abilities of Four Corvids Based on Ecology

Species	Ecology			Predictions	
	Climatic conditions	Social structure	Spatial memory	Comparison of the sexes	Social cognition
Clark’s Nutcracker	Harsh	Simple	Excellent	N. D. ^a	Low
Pinyon Jay	Harsh	Complex	Excellent	M+++ ^b	Excellent
Scrub Jay	Mild	Simple	Modest	N. D. ^a	Low
Mexican Jay	Mild	Complex	Modest	N. D. ^a	Excellent

^a No difference
^b Superior in males

They use their long, heavy, sharp bills to open green pine cones and extract their seeds. When the pine cone crop is large, an individual Clark's Nutcracker may harvest and store between 22,000 and 33,000 individual pine seeds in over 2000 unique cache sites. These birds are known to discriminate edible from empty and inedible seeds by "bill weighing" and "bill clicking," and they also use seed-coat color to discriminate between edible and inedible seeds (i.e. yellow-hulled seeds are empty, chocolate brown-hulled seeds are full). Nutcrackers possess a sublingual pouch (Bock et al., 1973) in which they can transport a volume of up to 28.5 ml, or about 90 medium-sized pinyon pine seeds. Nutcrackers range widely in search of pine cones and have been observed carrying a full pouch of seeds as far as 22 km. Seeds are cached on territories (personal observation of RPB) and also on "communal" areas, which are wind-swept, southeast-facing slopes where snow is either blown away or melts earlier in the spring. Birds appear to cache from sunrise to sunset until the crop is depleted or until snow covers the ground and inhibits caching. Nutcrackers have the ability to accurately find their own hidden seed caches up to 9 months after having made them (Vander Wall and Hutchins, 1983; Tomback, 1980).

Pinyon Jays live in the southwestern United States at lower elevations (1850-2200 m) than nutcrackers, but they experience a harsh winter climate as well. Pinyon Jays rely heavily on cached pine seeds for winter food, taking between 70 and 90 percent in their diet from November through February (Ligon, 1978). Pinyon Jays use their sharp, pointed bills to extract pine seeds from green cones. The bill is featherless at its base, thus effectively increasing the feather-free length of the bill for reaching into sap-laden cones. As cones open, Pinyon Jays can discriminate between inedible and edible seeds by visual inspection, bill weighing, and bill clicking (Ligon and Martin, 1974). Pinyon Jays carry seeds in an esophagus that is distensible for about two-thirds of its length. This structure has a maximum capacity of about 17.3 ml, or about 39 medium-sized pinyon pine seeds. Pinyon Jays spend their entire life in a flock that may vary in number from 40 to 400 conspecifics. Flocks travel over a large home range each autumn in search of ripening seeds. Birds carrying full loads of seeds have been observed flying as far as 20 km to a caching location. Seeds are harvested, transported, and cached by members of the flock working together. Pinyon Jay flocks typically cache on the same plots of ground (traditional caching areas) year after year (Marzluff and Balda, 1992). On these areas the jays seem to prefer to cache near tree trunks where snow melt is rapid. We calculated that when cones are common a single Pinyon Jay could

cache over 25,000 pine seeds in a year (Balda and Bateman, 1972). Ligon (1978) estimated that a single flock of birds in central New Mexico cached up to 4.5 million seeds in a single autumn. Birds continue to cache seeds until the seed crop is depleted or snow prevents them from caching in the substrate. Seeds are recovered throughout the winter and into the next spring. Like nutcrackers, Pinyon Jays breed early in the season, with nest construction occurring as early as late February in years when pine seeds are particularly abundant. Pine seeds may make up between 10 and 32 percent of the nestlings' diet (Ligon, 1978; Bateman and Balda, 1973).

Of our study species, Scrub Jays and Mexican Jays inhabit the lowest elevations (1650-2200 m) and experience the mildest climatic conditions. Concomitantly, they are not as well equipped morphologically or behaviorally for the harvest, transport, caching, and recovery of pine seeds. These species must wait for the pine cones to open before they can extract seeds, as their bills are not sufficiently sharp or sturdy for chiseling open green cones. Scrub Jays partially compensate for this lack by kleptoparasitizing seeds and cones from Clark's Nutcrackers (Vander Wall and Balda, 1981), waiting until nutcrackers have pried open the cone scales of green cones. Then, screaming frantically, they fly at the nutcrackers that, startled, drop the cones and fly off. Scrub Jays do not appear to be motivated to cache (Hall, unpublished data) as strongly as the above two species and have no special structure for carrying seeds, usually carrying between one and five seeds in their mouths and bills. Balda (1987) estimated a single Scrub Jay may cache up to 6000 seeds in one autumn. Seeds do not appear to be evaluated for quality, nor do birds fly more than a few km to harvest or cache them. These jays harvest cached seeds throughout the winter and into the spring. They do not breed particularly early, nor do they feed pine seeds to their nestlings.

These ecological differences led us to predict that nutcrackers and Pinyon Jays would be able to recover their hidden caches of food more accurately than Scrub Jays and Mexican Jays (Table 1, column 4). This prediction has been tested in several experiments (Balda and Kamil, 1989; Bednekoff et al., in press) conducted under standardized conditions in a large experimental room. Nutcrackers and Pinyon Jays outperformed Scrub Jays in a test of cache recovery accuracy (Figure 1), recovering food they had cached earlier with fewer errors (i.e., visits to locations where food had not been stored). In subsequent comparative studies, Mexican Jays also performed poorly as compared to nutcrackers and Pinyon Jays (Balda et al., unpublished).

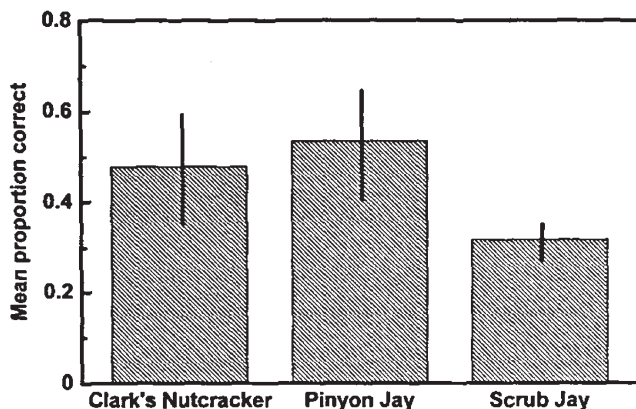


Figure 1. Results of accuracy in cache recovery for three corvid species: Clark's Nutcrackers ($n = 7$), Pinyon Jays ($n = 7$), and Scrub Jays ($n = 7$). Birds were allowed to make eight caches selected from 15 possible sites and to recover them after an 8-day retention interval. (From Balda and Kamil, 1989)

These cache-recovery results are consistent with an adaptive explanation of species differences in spatial memory. That is, the comparative differences in cache-recovery accuracy we observed may have been attributable to species differences in the ability to remember spatial information. However, no single test of species differences in cognitive abilities can be regarded as conclusive (Kamil, 1988a) because many non-cognitive factors could produce a between-species difference on any particular test. This problem arises because of what psychologists call the learning-performance distinction. We are interested in cognitive capacity, but we can only measure cognitive capacity through performance in specific experiments; yet there are many noncognitive factors, such as motivation, that can affect performance. Therefore, we must always be aware of the possibility that poor performance by some of the species in a comparative experiment on cognitive ability may be due to noncognitive, contextual variables (Bitterman, 1960) rather than species differences in cognitive ability. Thus, multiple experimental tests, each measuring the relevant cognitive ability in a different way, must be employed.

Following this logic, we conducted several subsequent studies using different tasks to obtain independent measures of the spatial-memory abilities of these species. In one set of studies, we used procedures modeled on the radial arm maze developed by Olton and Samuelson (1976) with rats. A radial arm maze has multiple arms (usually eight) that radiate outwards from a central platform. A single piece of food is placed at the end of each arm, and the rat is allowed to search for the food. The

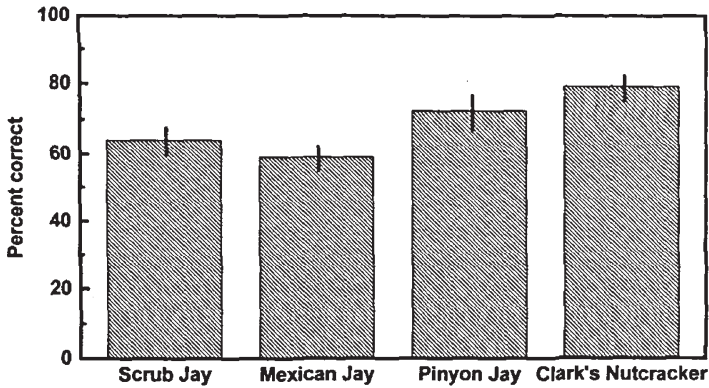


Figure 2. Results of acquisition testing for four corvid species: Clark's Nutcrackers ($n = 6$), Pinyon Jays ($n = 6$), Scrub Jays ($n = 6$), and Mexican Jays ($n = 6$) in a radial maze. Figure presents average percent correct for trials 49 through 60. Chance is 50%. (From Kamil et al., 1994)

dependent variable is the number of repeat visits made before finding all eight pieces of food. The greater the spatial memory, the fewer repeat visits made as rats learn to avoid arms previously visited. Rats solve this problem very efficiently, typically making no more than one or two errors. A series of control experiments has since demonstrated that this performance is based on spatial memory (Beatty and Shavalia, 1980; Olton and Collison, 1979). In our adaptation of this procedure, we used a room with 12 holes in the floor, arranged in a circle. Each hole could either be filled with sand or capped with a wooden plug. Each day, a bird was allowed into the room twice. During the first entry, four randomly selected holes (a different set each day) were available and the bird was allowed to visit and recover food from each of them. The bird was then removed from the room for 5 min. During this retention interval all signs of digging were cleaned up around the four original holes. When the bird re-entered the room it encountered eight open holes, the four holes it had probed during its previous visit to the room and four randomly-selected, newly-opened holes. Food was present only in the newly-opened holes. Thus, the birds had to remember and avoid the previously visited locations in order to find food. Nutcrackers and Pinyon Jays readily probed the newly opened holes and avoided the holes previously visited (Kamil et al., 1994; Figure 2). Nutcrackers and Pinyon Jays also performed this task more rapidly and more accurately than either of the two *Aphelocoma* species.

In another set of studies, operant procedures known as nonmatching-to-sample were used. In a typical spatial nonmatching-to-sample ex-

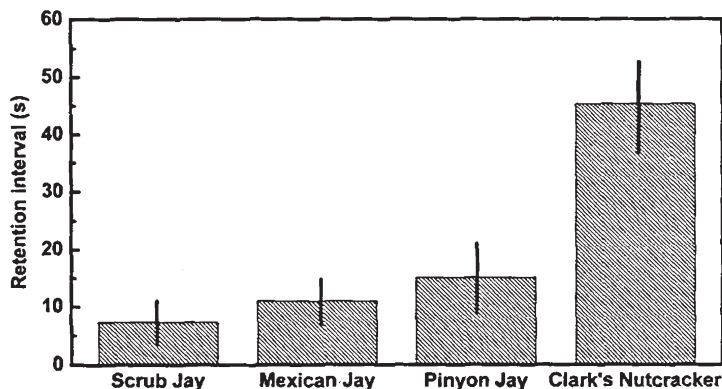


Figure 3. Results of comparative, operant, spatial, nonmatching-to-sample test for four corvid species: Clark's Nutcrackers ($n = 4$), Pinyon Jays ($n = 4$), Scrub Jays ($n = 41$), and Mexican Jays ($n = 2$). Figure presents retention interval after a mean of 100 trials. (From Olson et al., 1995)

periment, birds receive many trials per day in an operant chamber containing two pecking keys. As in the radial maze analogue experiment, each trial consists of two parts. In the first phase of the trial, one of the keys, randomly selected on each trial, is illuminated and the bird is required to peck at it in order to get a food reward. During the second part of the trial, both keys are illuminated. Reward is delivered only if the bird pecks first at the key that was not illuminated in phase one. As in the radial maze experiment, in order to receive reinforcement, the bird has to remember the location it "visited" previously, and then avoid it. After initial training, we measured how long the birds could remember this spatial location. Nutcrackers were accurate after much longer delays than were Scrub Jays (Olson, 1991). In a subsequent study, nutcrackers consistently outperformed all three of the other species (Olson et al., 1995; Figure 3).

In summary, the relative performance by the three corvid species during all three of these spatial memory tasks relates strongly to their respective degree of dependence on stored food.

Nutcrackers performed better than either Scrub Jays or Mexican Jays on all five studies, whereas in four of five studies Pinyon Jays performed more like nutcrackers than like the more closely related, but less cache-dependent, *Aphelocoma* species. In addition, behavior has been shown to covary with brain size. Neuroanatomical studies have shown differences associated with cache recovery in the size of the hippocampus, a part of the brain known to be involved in spatial cognition, including spatial

memory. Caching species have, on average, larger hippocampuses (relative to overall body or brain size, thus allowing for allometry) than non-caching species (Krebs et al. 1989; Sherry et al., 1989). Basil et al. (1996) have recently found that the relative size of the hippocampus in nutcrackers is larger than in Pinyon Jays, Mexican Jays, or Scrub Jays. Together, these behavioral and neuroanatomical studies appear to offer strong support for the hypothesis that species differences in spatial cognition correlate with environmental conditions.

However, an alternative hypothesis must be addressed, namely, that the nutcrackers and Pinyon Jays would outperform the other species on any laboratory task. This could be the case, for example, if these two species were simply more adaptable to laboratory conditions. Therefore we conducted an additional study in which members of all four species were tested on a nonspatial memory task. Our reasoning was that performance on this nonspatial task should be unrelated to cache recovery and that the results should show no correlation with dependence on stored food. The procedures were virtually identical to those of the spatial matching-to-sample experiment, except that birds were required to remember the color, not the position, of a stimulus. The results were as predicted: All four species were equally able to remember the color of the stimulus (Olson et al., 1995), demonstrating that the species differences in memory during the spatial studies are not universal, and may be limited to the spatial domain.

Although these species differences may be limited to the spatial domain, they appear to be quite general within that domain. That is, the results of radial maze and operant nonmatching-to-sample testing suggest that the effects of natural selection on spatial cognition are expressed in a wide variety of situations, not just cache recovery. This indicates that although the primary arena for the operation of natural selection may have been improving the recovery of cached food, the effects on spatial ability have been quite general, and possibly useful in a host of situations.

Finally, for maximum power, the comparative approach should include independent tests of hypotheses across independent lineages. In the case of spatial memory and dependence on stored food, work (similar to that on corvids) has also been carried out with members of the family Paridae. Within this taxon some species store and recover food over short intervals of time throughout fall and winter, others do not. Comparative research has revealed that the scatter-hoarding species consistently outperform noncaching species on a variety of tests of spatial cognition (Brodbeck, 1994; Clayton and Krebs, 1994a,b, 1993; Krebs et al., 1990).

The scatter-hoarding species also have larger hippocampal areas in the brain than do nonstoring species (Krebs et al., 1989, Sherry et al., 1989). The consistency of the results from the Paridae with the results from the Corvidae greatly increases our confidence in the generality of the link between intensity of food caching and spatial cognitive capacities. Interestingly, however, species differences found among the Paridae appear to be of much smaller magnitude than those found among the Corvidae. The reasons for this difference are not at all clear, although several possibilities deserve exploration through further comparative work using other species and families. One is body size. The corvids are generally much larger than the parids. This simple fact may allow for greater divergence in brain size among corvids. Another is the natural history of caching. While both parids and corvids are scatter hoarders, the time course of the cache-recovery cycle is quite different, at least in the species studied comparatively to date. Corvids such as nutcrackers and Pinyon Jays create all of their caches in the fall and recover some of them 6–9 months later. In contrast, many of the parids cache and recover repeatedly throughout the fall, winter, and spring, with much shorter intervals, on average, between caching and recovery. These different patterns appear to have influenced how natural selection has shaped the function and structure of spatial memory.

4.3. Sex Roles during Nesting

In this section, in order to demonstrate another way of applying the comparative approach to the study of cognition, we present a hypothesis about interspecific sex differences in spatial memory based on species differences in breeding biology. These predictions are currently under investigation, and regardless of the fate of this particular hypothesis, we believe that sex differences in cognitive ability will prove to be a fruitful area for investigation.

Recent behavioral and neuroanatomical research with microtine rodents and icterine blackbirds has shown that sex differences in spatial abilities and/or hippocampal volume vary across species in a manner that correlates with aspects of natural history (Sherry et al., 1993; Jacobs et al., 1990; Gaulin and FitzGerald, 1989, 1986). This led us to ask whether differences among the four corvid species in how the sexes allocate parental effort might be reflected in their spatial abilities. Clark's Nutcrackers and Pinyon Jays are among the earliest breeding birds in North America, and both rely heavily on cached seeds for reproduction. As nesting draws near, females are fed frequently by their mates and, after lay-

ing, eggs and nestlings must be attended virtually all the time because of cold, snowy, and inhospitable weather (Marzluff and Balda, 1992; Mewaldt, 1956). However, nutcrackers and Pinyon Jays differ substantially in the form of parental care provided by males and females.

Male Clark's Nutcrackers develop a brood patch, and they devote substantial time to incubation and brooding. Because incubation and brooding are shared, female nutcrackers are able to feed themselves and help provision the nestlings from seed caches made months previously (Mewaldt, 1956). Relying on the similarity in parental roles played by male and female nutcrackers, we predict that spatial abilities during breeding should be similar, and excellent, in both sexes.

In contrast, male Pinyon Jays do not develop a brood patch, and they do not incubate eggs or brood nestlings. Rather, they first feed the female, which spends almost all of her time on the nest during the 17 days of incubation and the first 12-15 days of brooding, and later feed her and as many as five offspring (Marzluff and Balda, 1992). Both sexes depend on stored food during the 4-month period from the end of caching in the fall until courtship feeding and nest construction in the late winter. However, once incubation begins, males must forage for themselves, their mates, and their offspring; females do little foraging. Because males forage largely by recovering stored food, they must remember the location of the seed caches for a longer time period than must females. This leads us to predict that Pinyon Jay females may forget spatial information more rapidly than males during the breeding season. More specifically, we predict that both sexes will recover caches with similar and high accuracy at intervals of less than 4 months, but males will perform more accurately than females after longer intervals.

Western Scrub Jays nest later in the spring, when conditions are milder. Although males provide most of the food for females and nestlings, food is not in short supply, and because of warmer temperatures females can leave their nests for extended periods and forage for themselves. In general, these jays do not rely heavily on hidden food stores to feed themselves, and, unlike Clark's Nutcrackers and Pinyon Jays, Scrub Jays do not feed seeds to their young. Their moderate level of dependence on caches probably accounts for their relatively modest spatial memory among the corvid species we have tested. Although males may occasionally feed themselves or provision females from cached food, we predict basically equal performance by male and female Scrub Jays in tasks requiring spatial memory.

The situation in Mexican Jays resembles that of Scrub Jays, except that yearlings often feed nestlings (Brown and Brown, 1990). As in Scrub Jays,

Mexican Jays do not feed seeds to their young, and food caches from the previous autumn are probably depleted or almost depleted by the time reproduction begins, so both males and females forage for recently produced food. We predict that males and females will not differ in tasks requiring spatial memory (Table 1, column 5).

4.4. Social Organization

Many have suggested that sociality in primates provided a crucial impetus for the evolution of complex cognition and/or abstract intelligence (Cheney and Seyfarth, 1990; Whiten and Byrne, 1988; Humphrey, 1976; Jolly, 1966; Chance and Mead, 1953), and the same may be true of birds. A number of different cognitive abilities could contribute to biological success within a social group. For example, individual recognition should be enhanced in social animals that live in large groups and repeatedly interact with the same individuals over time. If members of a group need to communicate information that solitary individuals do not, then signals used by social species may be more varied and complex and/or may be interpreted more subtly than signals used by solitary species. One way this may be accomplished is by using graded signals (Berger and Ligon, 1977; Morton, 1977; Marler, 1969). Living in a social unit may also allow for coordinated division of some tasks, such as serving as sentinels for predators (McGowan and Woolfenden, 1989; Balda and Bateman, 1971). Living in a complex social environment may also select for less direct or obvious skills. For example, social animals might be better able to classify, categorize, and/or quantify group members, based directly on previous experience with these individuals, than solitary animals. In addition, social animals may be better able than solitary animals to draw inferences about social relationships (e.g., dominance and kinship) between other group members without directly observing them (Cheney and Seyfarth, 1990). Although the hypothesis that cognition evolved in response to sociality was originally formulated for primates, there is nothing in this hypothesis that restricts it to any particular taxon (see Marler, this volume). Animals belonging to many taxa live in complex social groupings, and this hypothesis should apply quite generally to birds as well as primates and bees (Dukas and Real, 1991).

We propose that the comparative approach could be used to test the social evolution of cognition hypothesis quite broadly, within many taxa. We define social cognition to include the many cognitive skills that relate to the demands of groups living socially. By definition, a social animal must interact with other individuals in its social unit. If the results of

social interactions depend, in part, on the cognitive abilities of the participants, and if the outcomes of the interactions affect fitness, then natural selection can operate on cognitive abilities. Moreover, the nature of important social interactions probably varies as a function of type or size of the group. In that case, we would expect to find that differences in patterns of social living among species (or even populations) might be used to predict differences in cognitive abilities.

One important aspect of our approach is the comparison of closely related species that differ in social organization, and the four corvid species we study are excellent choices because they vary in complexity of their social units. Mexican Jays and Pinyon Jays are highly social, whereas nutcrackers and Scrub Jays are not. (Table 1, columns 3 and 6). Other comparisons are also possible. For example, solitary Scrub Jays from the western United States could be compared to their more social cooperatively breeding relatives in Florida (Woolfenden and Fitzpatrick, 1984). Florida Scrub Jays should show superior performance in tasks that require social cognition.

However, progress in this area depends upon a satisfactory answer to a basic question: Can cognitive skills that have been selected for in a social setting be expressed and studied outside of that setting? That is, can Acorn Woodpeckers (*Melanerpes formicivorus*) use the skills they employ in natural groups to analyze problems that do not involve other Acorn Woodpeckers? If social cognition cannot be generalized (or probed analytically) beyond the specific social context within which it evolved, then tests of social cognition are limited by the extent to which experimenters can control and manipulate events within social groups. This control is extremely difficult, particularly when the events of interest are by nature interactive. There is reason to be hopeful that social cognition will reflect more abstract or general skills that may be generalized to other, nonsocial circumstances. Primatologists have, in fact, suggested that: general abstract skills arose in a social context (Humphreys, 1976; Jolly, 1966). The basic challenges for future research in this area are to determine how cognitive abilities, including abstract ones, are used within social systems and to devise means to test for them in both social and nonsocial contexts.

The generalizability of social cognition is particularly critical to the comparative approach we have outlined. If the cognitive skills selected in the social sphere can be tested only in social settings, then the comparative approach will be almost impossible to employ. In social settings, it is extremely difficult to exercise experimental control over the environment. Yet such experimental control is necessary to present tasks to members of different species in an equivalent manner. Many expressly social

tasks may be impossible to present meaningfully to nonsocial species. In addition, a high degree of experimental control is necessary to evaluate the nature of cognitive processes. Therefore, the comparative approach to social cognition may be feasible only if at least some features of social cognition are generalizable to nonsocial settings. We recommend the development and use of abstract, nonsocial tasks designed to capture the essence of the kinds of discriminations, judgments, and inferences that must lie at the heart of social cognition.

For example, the ability to use transitive inference may be quite beneficial to an animal living in a large, stable group. Suppose that it is known that, with respect to social dominance, $A > B$, $B > C$, and $C > D$. If this system is transitive, then it follows that $A > C$, $A > D$, and $B > D$. Many workers (e.g., discussion in Cheney and Seyfarth, 1990) have speculated that social animals use transitive inference as a mechanism to deduce social relationships, especially dominance relationships, among members of their groups. If an animal lives in a large group, it is unlikely to witness dominance interactions among all possible pairs of individuals within the group. Therefore, it may benefit from being able to infer relationships between dyads that have not been directly observed. This benefit should increase as group size increases. If true, then animals such as Pinyon Jays, which live in large, stable groups, might be better able to use transitive inference than more solitary animals like nutcrackers or Scrub Jays. If the ability to use transitive inference were generalized beyond social settings, then social animals, when tested in nonsocial situations, should be better able to use transitive inference than more solitary animals. This test is quite feasible, as there are nonsocial, experimental methods for testing transitive inference in animals. Many of these techniques were developed with primates (e.g., Gillan, 1981). However, more recently, some controversial techniques using operant conditioning methodology have been developed with pigeons (*Columba livia*, see Wynne, 1995). We would predict that Pinyon Jays and Mexican Jays should perform consistently better than nutcrackers and Scrub Jays on abstract tests of transitive inference and other tests of social cognition. If true, these species differences will provide evidence for the evolution of social cognition and for the generalizability of these abilities. However, these experiments could fail either because social animals do not possess cognitive specializations or because social cognition cannot be applied to abstract, nonsocial tasks.

There are two reasons why we are optimistic that cognitive abilities in the social realm can be generalized to nonsocial tasks. First, our comparative studies of spatial memory, reviewed above, demonstrate that spatial

cognition in seed-caching corvids is not restricted to cache-recovery tasks, but is generally applicable to other spatial tasks. The differences among species undoubtedly evolved in the context of cache recovery, but they are also expressed in the radial-maze analogue (Kamil et al., 1994), and even in operant settings (Olson et al., 1995; Olson, 1991). The operant results are particularly impressive in this regard. Remembering a location on the wall of an operant chamber might seem strikingly different from remembering the location of a specific cache site created by an individual within a large home range in the wild. Yet nutcrackers consistently performed much better than Scrub, Pinyon, or Mexican Jays on this operant task.

Second, we have recently obtained comparative data on an arbitrary nonspatial task (Olson et al., 1995; Figure 4). This task required birds to view and peck at a colored spot on a TV screen. After a short time interval during which no spots were present, two colored spots were presented (in randomized spatial locations). The birds received food rewards when they pecked at the spot that was not the color of the original spot. The task was learned much faster by Pinyon Jays and Mexican Jays than by nutcrackers or Scrub Jays. (As described above, once all species had learned the task, they did not differ in the length of time that they could remember the color of the stimulus.) Although it is not clear how color nonmatching-to-sample might be related to social cognition, the social species learned it more rapidly. The among-species pattern obtained on this task was quite different from that obtained with spatial tasks. Thus, among species in this group, spatial cognition may vary as a function of

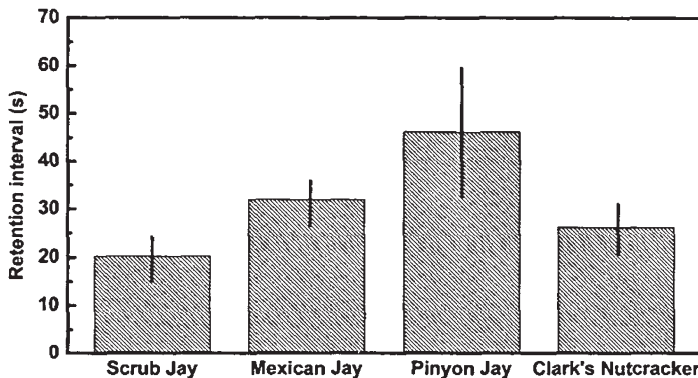


Figure 4. Results of comparative, operant, color, nonmatching-to-sample test for four corvid species: Clark's Nutcrackers ($n = 4$), Pinyon Jays ($n = 4$), Scrub Jays ($n = 4$), and Mexican Jays ($n = 3$). Figure presents retention interval for the last block of 100 trials. (From Olson et al., 1995)

cache dependence, while some aspects of nonspatial cognition vary as a function of sociality (Table 1, column 6).

A further complication arises when we consider that social factors might influence some aspects of spatial cognition and vice versa. In a recent set of experiments, Bednekoff and Balda (in press, 1996a,b; Figure 5) allowed Clark's Nutcrackers, Pinyon Jays, and Mexican Jays to observe conspecifics as they cached, and then allowed them to search for these hidden caches 1 or 2 days later. During the retention interval, all signs of activity at the cache sites were removed. Mexican Jays and Pinyon Jays were more accurate than nutcrackers on this task, even though nutcrackers were most accurate when recovering caches they created themselves. Thus, social organization may affect the ability to infer and/or remember a spatial location made salient by a conspecific and observed from a distance. However, this experiment also demonstrates the difficulty of using social tasks to test the social cognition hypothesis. The difference between the social jays and the nutcrackers could be the result of social animals paying more attention to conspecifics than do nonsocial animals, rather than their having a better memory for observed caches. Controlled tests with nonsocial stimuli signaling cache location could eliminate this alternative explanation.

These results appear to demonstrate that different mental capabilities can be affected independently by different selective pressures. This is consistent with the suggestions that there are different types of memory systems (Sherry and Schacter, 1987), or that human intelligence consists

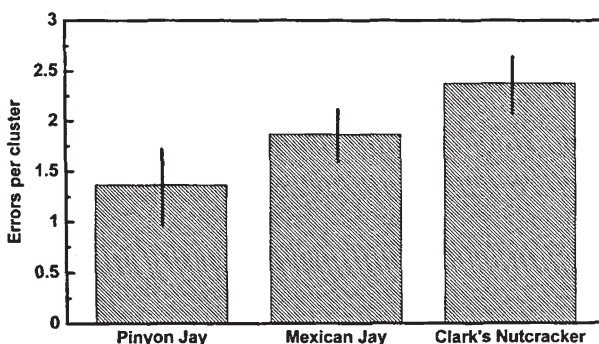


Figure 5. Comparison of three species of seed-caching corvids: Pinyon Jays ($n = 12$), Clark's Nutcrackers ($n = 10$), and Mexican Jays ($n = 12$), for accuracy of observers when recovering caches. Caches were created by conspecifics within sight of observers that were confined to cages. Recovery sessions took place 48 hrs later. During recovery each cache was a member of a cluster of six adjoining holes. Birds searching at random would be expected to average 2.5 errors per cluster when recovering caches.

of several independent components (e.g., Gardner, 1987). Ultimately, of course, selective pressures act on individuals and each individual has a unitary fitness value. Therefore, we should expect different selective pressures to interact to produce a suite of adaptive traits, including a set of cognitive abilities.

5. General Issues

Hypotheses about cognitive function framed in terms of natural history can obviously be formulated for many taxa. However, our approach presents some potential pitfalls and some difficult general issues. Below we discuss where and how our approach could be applied to other groups of birds and attempt to guide interested researchers around the pitfalls we foresee.

First is an assumption underlying the comparative approach to cognition that needs to be made explicit, namely, that there are costs associated with cognitive processes. Thus we expect animals to evolve only those cognitive processes whose benefits outweigh their costs. This assumption seems reasonable but has been little examined and deserves further thought and attention. For example, possessing a cognitive trait presumably involves possessing the neural tissue necessary to support it, and this should involve costs. One indication of cost is suggested by data on hippocampal size in seed-caching birds, data that revealed seasonal changes in hippocampal size. For at least some species of parids, the hippocampus appears to shrink during that time of year when caching does not occur (Barnea and Nottebohm, 1994).

There are other species in which studies of spatial cognition, sex differences in cognition, and social cognition would probably lead to interesting results. For example, several studies of nectar-feeding birds that feed on small, slowly repleting flowers suggest that these birds possess the spatial memory abilities to allow them to systematically exploit this type of nectar distribution (Armstrong et al., 1987; Wunderle and Martinez, 1987; Cole et al., 1982; Kamil, 1978). It would be interesting to know whether the spatial abilities of other nectar feeders, such as "trapliners" that feed on large, rapidly repleting flowers might lack the same level of spatial skills (as suggested by Gill, 1988).

Males and females often play strikingly different roles in nature, and the crucial choices and life history tradeoffs that determine fitness may be very different for the two sexes. Sex differences in specific cognitive abilities could be present in any or all species in which sex roles differ greatly. Field workers will have no trouble identifying situations in which differ-

ent sex roles may well have cognitive consequences or underpinnings. For example, female Brown-headed Cowbirds (*Molothrus ater*) search out the nests of potential hosts, returning to these nests at the proper time in order to lay their eggs in them. Males do nothing of the sort. Neuroanatomical work has verified that the area of the brain involved in spatial memory is larger in female than in male eastern cowbirds (Sherry et al., 1993). We expect that female cowbirds will outperform males on laboratory tests of spatial abilities.

At first glance, the social cognition hypothesis seems applicable to every situation in which three or more animals are gathered together. This is not necessarily so. The social cognition hypothesis rests on the importance of social interactions among individuals. Therefore the development of social cognition is dependent on the complexity of interactions, rather than the number of animals seen together. Therefore workers interested in the social-cognition hypothesis need to determine how groups are structured and to identify the types of social interactions important to individuals in groups before engaging in tests of this hypothesis. We expect that this hypothesis will apply most appropriately to cohesive, long-lasting groups that contain both related and unrelated individuals. For example, Acorn Woodpeckers (Koenig and Stacey, 1990), White-fronted Bee-eaters (*Merops bullockoides*) (Wrege and Emlen, 1994), and Green Woodhoopoes (*Phoeniculus purpureus*) (Ligon and Ligon, 1988, 1983) have this sort of group structure in some areas and engage in complex social interactions.

Long-term studies of banded populations of birds have revealed a wide diversity of social systems. As our knowledge of the diversity of social systems grows, we should be able to refine the social cognition hypothesis. Potentially, our single hypothesis will become a family of hypotheses that reflect the diversity of interactions within social groups of different organizations. For instance, Pygmy Nuthatches (*Sitta pygmaea*) breed as pairs that are sometimes assisted by a few offspring from previous years. Thus, in the breeding season they appear to have only limited need for social cognition (Sydeman et al., 1988). When winter comes, however, another pattern emerges. Breeding pairs or family groups roost communally with other pairs or groups. The composition of the roosting group for any one night is influenced by ambient temperature, snowfall, and available roosting cavities. Each pair or family group has a complex set of alliances that determine with which birds it will roost. These alliances are not based on proximity, as home ranges of allies are not always adjacent to one another (Guntert et al., 1988; Guntert, unpublished data). Long-term studies of marked individuals are likely to reveal greater social complexity than would be expected to be indicated by short-term

studies. For example, the clan system of elephants was revealed only after observation of known individuals over many years (Moss, 1988). Although they may take less absolute time, field studies of similar intensity and relative duration are necessary to reveal the true complexity of the social systems of many bird species.

6. Phylogenetic Considerations

We have thus far emphasized understanding cognitive abilities by understanding their current ecological functions. Although we believe this is central to the research program we propose, phylogenetic considerations also play a role, particularly when comparative studies are undertaken. For example, we claimed that cache dependence had led to cognitive convergence in Clark's Nutcrackers and Pinyon Jays. We make this claim only because we know that these species are distantly related and have closer relatives that are less cache dependent (see Figure 6, based

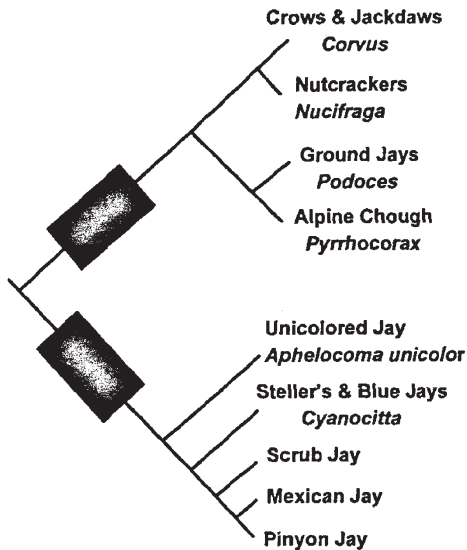


Figure 6. Schematic phylogeny of selected corvids, redrawn from Hope (1989). Branch lengths have been approximated to simplify presentation. The black boxes conceal the many other branchings of the Old World corvids (top) and New World jays (bottom). Pinyon Jays and nutcrackers have diverged in many ways from their respective close relatives and converged on adaptations for storing and retrieving pine seeds. Note that bird names have not been changed to reflect this new phylogeny.

on Hope, 1989). Pinyon Jays are most closely related to Mexican Jays and Scrub Jays. Clark's Nutcrackers are most closely related to Eurasian Nutcrackers. Therefore, we ascribe the similarities between Clark's and Eurasian Nutcrackers (Balda, 1980) to common ancestry. On the other hand, the two nutcracker species are closely related to Alpine Choughs (*Pyrrhocorax graculus*) and Jackdaws (*Corvus monedula*), two species that cache hardly at all (Healy and Krebs, 1992). We can be confident that nutcrackers and Pinyon Jays have evolved their excellent spatial memories independently because each is more closely related to species that lack such excellent memories than they are to each other. Based on their phylogeny, we attribute the similarity of performance by nutcrackers and Pinyon Jays to cognitive convergence.

Comparative studies of adaptation require knowledge of both the evolutionary relationships and the distribution of traits among the taxa (Harvey and Pagel, 1991). If we had data on the cognitive skills of many species, we could apply sophisticated methods to entire groups of organisms (e.g. Felsenstein, 1988, 1985). At this time we are just beginning to gather the relevant data, and, because this effort will require intensive testing of each species, study species should be chosen with care. We suggest that the most powerful way to proceed is to test closely related organisms that currently experience different ecological demands. For example, our explorations of social cognition would be enormously strengthened by adding one species, the Jackdaw, to our comparisons. Since Mexican Jays and Pinyon Jays are probably each other's closest relatives (Hope, 1989, Figure 6), we should count the performance of these two versus that of Scrub Jays as a single test of social cognition. Jackdaws are highly social and closely related to nutcrackers. Therefore comparing Jackdaws and nutcrackers would constitute an independent test of the social cognition hypothesis.

The most rigorous application of our recommendation calls for testing either highly divergent populations of the same species or sister species. We consider this the most rigorous because all comparative tests depend upon the "all other things are equal" assumption. This assumption is most likely to be true when the ecologically divergent populations being compared are most closely related. We hypothesized that the social Florida Scrub Jays should differ in social cognition from the asocial western Scrub Jays. Although many populations may not have accumulated sufficient genetic variation, become sufficiently separated from other populations, or had enough time to achieve a precise match between cognitive abilities and current ecological demands, we stand by this prediction. We know that Scrub Jays have repeatedly evolved bill shapes appropriate for different environments (Peterson, 1993). We see no reason why the ma-

chinery on the front of birds' skulls should be amenable to natural selection, but the machinery inside their skulls should not.

7. Ontogenetic Considerations

Genetic endowment (phylogeny) and experience (ontogeny) combine to prepare a caching bird with the ability to locate its caches. Our work to date has focused on species differences in the performance of wild-caught adults on a variety of spatial memory tasks. These results are consistent with the existence of a genetically based component contributing to the species differences. However, because all behavior is the result of both genetic endowment and experience, a complete investigation will require studies to delineate the role of ontogeny and the nature of the interaction between genetic and experiential factors.

We already know that ontogeny is important to the development of the behavioral system that results in cache recovery. During cache recovery experiments in the laboratory (Dimmick, 1993), wild-caught nutcracker adults are more accurate than wild-caught yearlings, and wild-caught juveniles are the least accurate of the three age groups. Although these experiments confounded the effects of maturation and experience, which probably interact, they suggest an ontogenetic process. Further information is provided by developmental neuroanatomical and behavioral work on corvids and parids. The hippocampus continues to increase in volume in fledglings of species that store food, but not in species that rarely, if ever, store food (Healy et al., 1994; Healy and Krebs, 1992). Moreover, behavioral research has confirmed that the ontogeny of cache recovery in parids depends on both maturation and experience (Clayton, 1992, 1994, 1995a,b) and that normal growth of the hippocampus requires experience in caching and recovering food (Clayton, 1995b).

Future research needs to use a combination of comparative and developmental strategies to achieve a full understanding of the phylogeny and ontogeny of spatial memory in seed-storing birds. In particular, studies need to be done in which different species are each raised under a variety of conditions. This research strategy will allow both species and environmental effects on brain and cognitive abilities to be assessed.

8. Summary

We have outlined a general approach to studying animal cognition in which natural history provides the background for understanding cogni-

tion. We have used this approach to formulate three sets of comparative predictions based on the natural histories of four corvid species. These hypotheses predict species differences in spatial memory, in the pattern of sex differences in spatial memory, and in social cognition. Taken together, these predictions illustrate a strategy for studying cognition in an ecological framework. This strategy tests the premise that different selection pressures can mold different mental capabilities. Animals should have cognitive abilities appropriate for the problems they must solve in nature. The distribution of cognitive abilities among species will not be completely understood without understanding the role these abilities play in ecological settings. However, these abilities must be studied experimentally, utilizing organisms with well-studied natural histories, so that the results can then be understood within a valid ecological context. Birds are a particularly suitable taxon for the use of this strategy because they are extremely well-known, highly diverse, and easy to study.

Acknowledgments

This work was sponsored by NSF grants BNS-9008803, DEB-9504103, DEB-9421807 and MH-44200. We thank Reuven Dukas, Lee Gass, Donald Kroodsma, Bruce Pavlick, Irene Pepperberg, Wayne Romonchuk, Sara Shettleworth, Jennifer Templeton, and Glen Woolfenden for thoughtful suggestions on earlier drafts of this manuscript. Arla Hile was extremely helpful in all aspects of thinking about, writing, and preparing the manuscript.

References

- Anderson, J. R., 1990, *Cognitive Psychology and Its Implications*, 3rd edition, Freeman and Co., New York.
- Andersson, M., 1982, Female choice selects for extreme tail length in a widowbird, *Nature* 299:818-820.
- Armstrong, D. P., Gass, C. L., and Sutherland, G. D., 1987, Should foragers remember where they've been? Explorations of a simulation model based on the behavior and energetics of a territorial hummingbird, in: *Foraging Behavior* (A. C. Kamil, J. R. Krebs, and H. R. Pulliam, eds.), Plenum Press, New York, pp. 563-586.
- Balda, R. P., 1980, Recovery of cached seeds by a captive *Nucifraga caryocatactes*, *Z. Tierpsychol.* 52:331-346.
- Balda, R. P., 1987, Avian impact on pinyon-juniper woodland, in: *Proceedings—Pinyon-juniper Conference* (R. L. Everett, ed.), U.S.D.A. Gen. Tech. Report INT-215, pp. 526-533.
- Balda, R. P., and Bateman, G. C., 1971, Flocking and annual cycle of the Pinyon Jay (*Gymnorhinus cyanocephalus*), *Condor* 73:287-302.

- Balda, R. P., and Bateman, G. C., 1972, The breeding biology of the Pinyon Jay, *Living Bird* 11:5-42.
- Balda, R. P., and Kamil, A. C., 1989, A comparative study of cache recovery by three corvid species, *Anim. Behav.* 38:486-495.
- Barnea, A., and Nottebohm, F., 1994, Seasonal recruitment of hippocampal neurons in adult free-ranging Black-capped Chickadees, *Proc. Natl. Acad. Sci.* 91:11217-11221.
- Basil, J. A., Kamil, A. C., Balda, R. P., and Fite, K. V., 1996, Differences in hippocampal volume among food-storing corvids, *Brain Behav. Evol.* 47:156-164.
- Basolo, A. L., 1990, Female preference predates the evolution of the sword in swordtail fish, *Science* 250:808-810.
- Bateman, G. C., and Balda, R. P., 1973, Growth, development, and food habits of young Pinyon Jays, *Auk* 90:39-61.
- Beatty, W. W., and Shavalia, D. A., 1980, Spatial memory in rats: time course of working memory and effect of anesthetics, *Behav. Neur. Biol.* 28:454-462.
- Bednekoff, P. A., and Balda, R. P., 1996a, Social caching and observational spatial memory in Pinyon Jays, *Behaviour*, 133:807-826.
- Bednekoff, P. A., and Balda, R. P., 1996b, Observational spatial memory in Clark's Nutcrackers and Mexican Jays, *Anim. Behav.* 52:833-839.
- Bednekoff, P. A., Balda, R. P., Kamil, A. C., and Hile, A., Long term spatial memory in four seed-caching corvid species, *Anim. Behav.*, in press.
- Beecher, M. D., Campbell, S. E., and Burt, J. M., 1994, Song perception in the Song Sparrow: birds classify by song type but not by singer, *Anim. Behav.* 43:283-287.
- Benkman, C. W., Balda, R. P., and Smith, C. C., 1984, Adaptations for seed dispersal and the compromises due to seed predation in limber pine, *Ecology* 65:632-642.
- Berger, L. R., and Ligon, J. D., 1977, Vocal communication and individual recognition in the Pinon Jay *Gymnorhinus cyanocephalus*, *Anim. Behav.* 25:567-584.
- Bitterman, M. E., 1960, Toward a comparative psychology of learning, *Am. Psychol.* 15:704-712.
- Bock, W. J., Balda, R. P., and Vander Wall, S. B., 1973, Morphology of the sublingual pouch and tongue musculature in Clark's Nutcracker, *Auk* 90: 491-519.
- Brodbeck, D. R., 1994, Memory for spatial and local cues: a comparison of a storing and a nonstoring species, *Anim. Learn. Behav.* 22:119-133.
- Brooks, D. R., and McLennan, D. A., 1991, *Phylogeny, Ecology, and Behavior*, University of Chicago Press, Chicago.
- Brown, J. L., and Brown, E. R., 1981, Kin selection and individual selection in babblers, in: *Natural Selection and Social Behavior: Recent Research and New Theory* (R. D. Alexander and D. W. Tinkle, eds.), Chiron Press, New York, pp. 244-256.
- Brown, J. L., and Brown, E. R., 1990, Mexican jays: uncooperative breeding, in: *Cooperative Breeding in Birds* (P. B. Stacy, and W. D. Koenig, eds.), Cambridge University Press, Cambridge, England, pp. 267-288.
- Catchpole, C. K., 1986, Song repertoires and reproductive success in the Great Reed Warbler, *Acrocephalus arundinaceus*, *Behav. Ecol. Sociobiol.* 19:439-445.
- Catchpole, C. K., Leisler, B., and Dittami, J., 1986, Sexual differences in the responses of captive Great Reed Warblers (*Acrocephalus arundinaceus*) to variation in song structure and size, *Ethology* 72:69-77.
- Chance, M. R. A., and Mead, A. P., 1953, Social behavior and primate evolution, *Evolution* 7:395-439.
- Cheney, D. L., and Seyfarth, R. M., 1990, *How Monkeys See the World*, University of Chicago Press, Chicago.

- Clayton, N. S., 1992, The ontogeny of food-storing and retrieval in Marsh Tits, *Behaviour* 122:11-25.
- Clayton, N. S., 1994, The role of age and experience in the behavioural development of food-storing and retrieval in Marsh Tits, *Parus polustris*, *Anim. Behav.* 47:1435-1444.
- Clayton, N. S., 1995a, Development of memory and the hippocampus: Comparison of food-storing and nonstoring birds on a one-trial associative memory task, *J. Neurosci.* 15:2796-2807.
- Clayton, N. S., 1995b, The neuroethological development of food-storing memory: a case of use it or lose it! *Behav. Brain Res.* 70:95-102.
- Clayton, N. S., and Krebs, J. R., 1993, Lateralization in Paridae: Comparison of a storing and a non-storing species on a one-trial associative memory task, *J. Comp. Physiol. A* 171:807-815.
- Clayton, N. S., and Krebs, J. R., 1994a, One-trial associative memory: Comparison of food-storing and nonstoring species of birds, *Anim. Learn. Behav.* 22:366-372.
- Clayton, N. S., and Krebs, J. R., 1994b, Memory for spatial and object-specific cues in food-storing and non-storing birds, *J. Comp. Physiol. A* 174:371-379.
- Cole, S., Hainsworth, F. R., Kamil, A. C., Mercier, T., and Wolf, L. L., 1982, Spatial learning as an adaptation in hummingbirds, *Science* 217:655-657.
- Crook, J. H., 1964, The evolution of social organization and visual communication in the weaverbirds (Ploceidae), *Behav. Suppl.* 10:1-178.
- Crook, J. H., 1965, The adaptive significance of avian social organization, *Sympos. Zool. Soc. London* 14:181-218.
- Davies, N. B., 1992, *Dunnock Behavior and Social Evolution*, Oxford University Press, Oxford, England.
- Dimmick, C. R., 1993, Life History and the Development of Cache-recovery Behaviors in Clark's Nutcrackers, Unpublished Ph. D. Dissertation, Northern Arizona University, Flagstaff.
- Dukas, R., and Real, L. A., 1991, Learning foraging tasks by bees: a comparison between social and solitary species, *Anim. Behav.* 44:269-274.
- Emlen, S. T., and Wrege P. H., 1988, The role of kinship in helping decisions among White-fronted Bee-eaters, *Behav. Ecol. Sociobiol.* 23:305-315.
- Endler, J. A., 1980, Natural selection on color patterns in *Poecilia reticulata*, *Evolution* 34:76-91.
- Falls, J. B., 1992, Playback: a historical perspective, in: *Playback and Studies in Animal Communication* (P. K. McGregor, ed.), Plenum Press, New York, pp. 11-33.
- Felsenstein, J., 1985, Phylogenies and the comparative method, *Am. Nat.* 125:1-15.
- Felsenstein, J. 1988, Phylogenies and quantitative characters, *Ann. Rev. Ecol. System.* 19:445-471.
- Gardner, H., 1987, *The Mind's New Science: A History of the Cognitive Revolution*, 2nd. edition, Basic Books, New York.
- Gaulin, S. J. C., and FitzGerald, R. W., 1986, Sex differences in spatial ability: an evolutionary hypothesis and test, *Amer. Natl.* 127:74-88.
- Gaulin, S. J. C., and FitzGerald, R. W., 1989, Sexual selection for spatial-learning ability, *Anim. Behav.* 37:322-331.
- Gill, F. B., 1988, Trapline foraging by Hermit Hummingbirds: competition for an undefended, renewable resource, *Ecology* 69:1933-1942.
- Gillan, J., 1981, Reasoning in the chimpanzee, II. Transitive inference, *J. Exp. Psychol. Anim. Behav. Proc.* 7:150-164.

- Giuntoli, M., and Mewaldt, L. R., 1978, Stomach contents of Clark's Nutcrackers collected in western Montana, *Auk* 95:595-598.
- Goodwin, D., 1986, *Crows of the World*, 2nd edition, British Museum of Natural History, London.
- Goss-Custard, J. D., 1981, Feeding behavior of Red Shank, *Tringa totanus*, and optimal foraging theory, in: *Foraging Behavior: Ecological, Ethological, and Psychological Approaches* (A. C. Kamil and T. D. Sargent, eds.), New York, Garland Press, pp. 115-134.
- Grant, B. R., and Grant, P. R., 1989, Natural selection in a population of Darwin's Finches, *Am. Nat.* 133:377-393.
- Guntert, M., Hay, D. B., and Balda, R. P., 1988, Communal roosting of the Pygmy Nut-hatch: a winter survival strategy, in: *Proceedings of the International Ornithological Congress* (H. Ouellet, ed.), University of Ottawa Press, Ottawa, pp. 1963-1972.
- Harvey, P. H., and Pagel, M. D., 1991, *The Comparative Method in Evolutionary Biology*, Oxford University Press, Oxford, England.
- Healy, S. D., and Krebs, J. R., 1992, Food storing and the hippocampus in corvids: amount and volume are correlated, *Proceedings of the Royal Society of London B* 248:241-245.
- Healy, S. D., Clayton, N. S., and Krebs, J. R., 1994, Development of hippocampal specialization in two species of tits (*Parus* spp.), *Behav. Brain Res.* 61:23-28.
- Herrnstein, R. J., 1985, Riddles of natural categorization, in: *Animal Intelligence* (L. Weiskrantz, ed.), Clarendon Press, Oxford, England, pp. 129-142.
- Hilton, S. C., and Krebs, J. R., 1990, Spatial memory of four species of *Parus*: performance in an open-field analogue of a radial maze, *Quart. J. Exper. Psychol.* 42B:345-368.
- Hollis, K. L., 1984, The biological function of Pavlovian conditioning: the best defense is a good offense, *J. Exper. Psychol.: Anim. Behav. Proc.* 10:413-425.
- Hope, S., 1989, Phylogeny of the Avian Family Corvidae, Unpublished Ph. D. Dissertation, City University of New York, New York.
- Humphrey, N. K., 1976, The social function of intellect, in: *Growing Points in Ethology* (P. P. G. Bateson and R. A. Hinde, eds.), Cambridge University Press, Cambridge, England, pp. 303-317.
- Jacobs, L. F., Gaulin, S. J. C., Sherry, D. F., and Hoffman, G. E., 1990, Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size, *Proc. Natl. Acad. Sci.* 87:6349-6352.
- Jolly, A., 1966, Lemur social behaviour and primate intelligence, *Science* 153:501-506.
- Kamil, A. C., 1978, Systematic foraging by a nectar-feeding bird, the Amakihi (*Loxops virens*), *J. Comp. Physiol. Psychol.* 92:388-396.
- Kamil, A. C., 1988a, A synthetic approach to the study of animal intelligence, in: *Comparative Perspectives in Modern Psychology*, Nebraska Symposium on Motivation, volume 35, (D. W. Leger, ed.), University of Nebraska Press, Lincoln, pp. 230-257.
- Kamil, A. C., 1988b, Experimental design in ornithology, in: *Current Ornithology*, volume 5 (D. M. Power, ed.), Plenum Press, New York, pp. 313-346.
- Kamil, A. C., and Yoerg, S. I., 1982, Learning and foraging behavior, in: *Perspectives on Ethology*, volume 5 (P. P. G. Bateson and P. H. Klopfer, eds.), Plenum Press, New York, pp. 325-364.
- Kamil, A. C., Jones, T. B., Pietrewicz, A. T., and Maudlin, J., 1977, Positive transfer from successive reversal training to learning set in Blue Jays, *J. Comp. Physiol. Psychol.* 91:79-86.
- Kamil, A. C., Balda, R. P., and Olson, D. J., 1994, Performance of four seed-caching corvid species in the radial-arm maze analog, *J. Comp. Psychol.: Anim. Behav. Proc.* 108:385-393.

- Ketterson, E. D., Nolan, V. Jr., Cawthorn, M. J., Parker, P. G., and Ziegenfus, C., 1996, Phenotypic engineering: using hormones to explore the mechanistic and functional bases of phenotypic variation in nature, *Ibis* 138:70-86.
- Koenig, W. D., and Stacy, P. B., 1990, Acorn Woodpeckers: group living and food storage under contrasting ecological conditions, in: *Cooperative Breeding in Birds* (P. B. Stacy and W. D. Koenig, eds.), Cambridge University Press, Cambridge, England, pp. 415-453.
- Konishi, M., and Nottebohm, F., 1969, Experimental studies in the ontogeny of avian vocalization, in: *Bird Vocalization: Their Relation to Current Problems in Biology and Psychology* (R. A. Hinde, ed.), Cambridge University Press, Cambridge, England, pp. 29-48.
- Krebs, J. R., and Davies, N., eds., 1984, *Behavioural Ecology*, Sinauer Associates Inc., Sunderland, Massachusetts.
- Krebs, J. R., Erichsen, T. J., Webber, M. I., and Charnov, E. L., 1977, Optimal prey selection in the Great Tit (*Parus major*), *Anim. Behav.* 25:30-38.
- Krebs, J. R., Kacelnik, A., and Taylor, P., 1978, Test of optimal sampling by foraging Great Tits, *Nature* 275:27-31.
- Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H., and Vaccarino, A. L., 1989, Hippocampal specialization of food-storing birds, *Proc. Natl. Acad. Sci.* 86:1388-1392.
- Krebs, J. R., Healy, S. D., and Shettleworth, S., 1990, Spatial memory of Paridae: Comparison of a storing and non-storing species, *P. ater* and *P. major*, *Anim. Behav.* 39:1127-1138.
- Krushinskya, N. L., 1966, Some complex forms of feeding behavior of nutcracker, *Nucifraga caryocatactes*, after removal of old cortex, *Z. Evoluz. Biochem. Fisiolog.* II, 563-568.
- Lack, D., 1947, *Darwin's Finches*, Cambridge University Press, Cambridge, England.
- Ligon, J. D., 1978, Reproductive interdependence of Pinyon Jays and pinyon pines, *Ecol. Monog.* 48:111-126.
- Ligon, J. D., and Ligon, S. H., 1983, Reciprocity in the Green Woodhoopoe (*Phoeniculus purpureus*), *Anim. Behav.* 31:480-489.
- Ligon, J. D., and Ligon, S. H., 1988, Territorial quality: key determinant of fitness in the group-living Green Woodhoopoe, in: *The Ecology of Social Behavior* (C. N. Slobodchekoff, ed.), Academic Press, San Diego, pp. 229-253.
- Ligon, J. D., and Martin, D. J., 1974, Pinyon seed assessment by the Pinyon Jay, *Anim. Behav.* 22:421-429.
- Lima, S. L., 1984, Downy Woodpecker foraging behavior: efficient sampling in simple stochastic environments, *Ecology* 65:166-174.
- Lorenz, K., 1941, Vergleichende bewegungsstudien bei Anatiden, *J. Ornithol.* 89:194-294.
- MacArthur, R. H., and Pianka, E. R., 1966, On optimal use of a patchy environment. *Am. Nat.* 100:603-609.
- Marler, P., 1969, Tonal quality of bird sounds, in: *Bird Vocalizations* (R. A. Hinde, ed.), Cambridge University Press, Cambridge, England, pp. 5-18.
- Marzluff, J. M., and Balda, R. P., 1992, *The Pinyon Jay: Behavioral Ecology of a Colonial and Cooperative Corvid*, Academic Press, London.
- McDonald, M. V., 1989, Function of song in Scott's Seaside Sparrow, *Ammodramus maritimus peninsulæ*, *Anim. Behav.* 38:468-485.
- McGowan, K. J., and Woolfenden, G. E., 1989, A sentinel system in the Florida Scrub Jay, *Anim. Behav.* 37:1000-1006.
- McLennon, D. A., and McPhail, J. D., 1989, Experimental investigations of the evolutionary significance of sexually dimorphic nuptial colouration in *Gasterosteus aculeatus* (L.): Temporal changes in the structure of the male mosaic signal, *Canad. J. Zool.* 67:1767-1777.

- McLennon, D. A., and McPhail, J. D., 1990, Experimental investigations on the evolutionary significance of sexually dimorphic nuptial colouration in *Gasterosteus aculeatus* (L.): The relationship between male colours and female behaviour, *Canad. J. Zool.* 68:482-492.
- Mewaldt, L. R., 1956, Nesting behavior of the Clark's Nutcracker, *Condor* 58:3-23.
- Morton, E. S., 1977, On the occurrence and significance of motivation-structural rules in some bird and mammal sounds, *Am. Nat.* 111:855-869.
- Morse, D. H., and Fritz, R. S., 1987, The consequences of foraging for reproductive success, in: *Foraging Behavior* (A. C. Kamil, J. R. Krebs, and H. R. Pulliam, eds.), Plenum Press, New York, pp. 443-455.
- Moss, C. J., 1988, *Elephant Memories*, Houghton Mifflin, Boston.
- Myberg, A. A., Jr., and Riggio, R. J., 1985, Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*), *Anim. Behav.* 33:411-416.
- Olson, D. J., 1991, Species differences in spatial memory among Clark's Nutcrackers, Scrub Jays, and Pigeons, *J. Exper. Psychol.: Anim. Behav. Proc.* 104:326-334.
- Olson, D. J., Kamil, A. C., Balda, R. P., and Nims, P. J., 1995, Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory, *J. Comp. Psychol.: Anim. Behav. Proc.* 109:173-181.
- Olton, D. S., and Collison, C., 1979, Intramaze cues and "odor trails" fail to direct choice behavior on an elevated maze, *Anim. Learn. Behav.* 7:221-223.
- Olton, D. S., and Samuelson, R. J., 1976, Remembrance of places passed: spatial memory in rats, *J. Exper. Psychol.: Anim. Behav. Proc.* 2:97-116.
- Pepperberg, I. M., 1990, Some cognitive capacities of an African Grey Parrot (*Psittacus erithacus*), in: *Advances in the Study of Behavior* (P. J. B. Slater, J. S. Rosenblatt, and C. Beer, eds.), Academic Press, New York, pp. 357-409.
- Peterson, A. T., 1993, Adaptive geographical variation in bill shape of Scrub Jays, *Am. Nat.* 142:508-527.
- Pettifor, R. A., Perrins, C. M., and McCleery, R. H., 1988, Individual optimization clutch size in great tits, *Nature* 336:160-152.
- Pulliam, H. R., 1980, Do Chipping Sparrows forage optimally?, *Ardea* 68:75-82.
- Pulliam, H. R., 1981, Learning to forage optimally, in: *Foraging Behavior: Ecological, Ethological, and Psychological Approaches* (A. C. Kamil, and T. D. Sargent, eds.), Garland Press, New York, pp. 379-388.
- Real, L. A., 1991, Animal choice behavior and the evolution of cognitive architecture, *Science* 253:980-986.
- Roitblat, H. L., Beaver T., and Terrace, H., eds., 1984, *Animal Cognition*, Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- Sherry, D. F., and Schacter, D. L., 1987, The evolution of multiple memory systems, *Psychol. Rev.* 94:439-454.
- Sherry, D. F., and Vaccarino, A. L., 1989, Hippocampal aspiration disrupts cache recovery in Black-capped Chickadees, *Behav. Neurosci.* 103:308-318.
- Sherry, D. F., Vaccarino, A. L., Buckenham, K., and Herz, R., 1989, The hippocampal complex of food-storing birds, *Brain Behav. Evol.* 34:308-317.
- Sherry, D. F., Forbes, M. R. L., Khurgel, M., and Ivy, G. O., 1993, Females have a larger hippocampus than males in the brood-parasitic Brown-headed Cowbird, *Proc. Natl. Acad. Sci.* 90:7839-7843.
- Shettleworth, S. J., 1984, Learning and behavioral ecology, in: *Behavioral Ecology*, 2nd edition, (J. R. Krebs, and N. B. Davies, eds.) Sinauer Associates, Sunderland, Massachusetts, pp. 170-194.

- Shettleworth, S. J., 1993, Where is the comparison in comparative cognition? *Psychol. Sci.* 4:179-184.
- Spector, D., 1992, Wood-warbler song systems: a review of paruline singing behavior, in: *Current Ornithology*, Volume 9, (D. M. Powers, ed.), pp. 199-238.
- Staicer, C. A. 1991, Characteristics, use, and significance of two singing behaviors in Grace's Warbler (*Dendrocia graciae*), *Auk* 106:49-63.
- Stoddard, P. K., 1996, Vocal recognition of neighbors by territorial passerines, in: *Ecology and Evolution of Acoustic Communication in Birds*, (D. E. Kroodsma, and E. H. Miller, eds.) Cornell University Press, Ithaca, New York, pp. 356-374.
- Sydeman, W. J., Guntert, M., and Balda, R. P., 1988, Annual reproductive yield in the cooperative Pygmy Nuthatch (*Sitta pygmaea*), *Auk* 105:70-77.
- Tinbergen, N., 1960, *The Herring Gull's World*, Doubleday, Garden City, New York.
- Tinbergen, N., 1963, The shell menace. *Nat. Hist.* 72:28-35.
- Tinbergen, N., Impeken, M., and Frank, D., 1967, An experiment on spacing-out as a defense against predation, *Behaviour* 28:307-321.
- Tombback, D. F., 1980, How nutcrackers find their seed stores, *Condor* 82:10-19.
- Vander Wall, S. B., and Balda, R. P., 1977, Coadaptations of the Clark's Nutcracker and the pinyon pine for efficient seed harvest and dispersal, *Ecol. Monog.* 47:89-111.
- Vander Wall, S. B., and Balda, R. P., 1981, Ecology and evolution of food-storage behavior in conifer-seed caching corvids, *Z. Tierpsychol.* 56:217-242.
- Vander Wall, S. B., and Hutchins, H. E., 1983, Dependence of Clark's Nutcracker (*Nucifraga columbiana*) on conifer seeds during the postfledgling period, *Can. Field Natl.* 97:89-111.
- Vaughan, J. W., 1988, Formation of equivalence sets in pigeons, *J. Exper. Psychol.: Anim. Behav. Proces.* 14:36-42.
- Weary, D. M., and Krebs, J. R., 1992, Great Tits classify songs by individual voice characteristics, *Anim. Behav.* 43:283-287.
- Welty, J. C., 1962, *The Life of Birds*, W. B. Saunders Co., New York, New York.
- Whiten, A., and Byrne, R. W., 1988, The Machiavellian intelligence hypotheses (editorial), in: *Machiavellian Intelligence* (R. W. Byrne, and A. Whiten, eds.), Clarendon Press, Oxford, England, pp. 1-9.
- Williams, G. C., 1966, *Adaptation and Natural Selection*, Princeton University Press, Princeton, New Jersey.
- Woolfenden, G. E., and Fitzpatrick, J. W., 1984, The Florida Scrub Jay: Demography of a Cooperative-breeding Bird, *Monogr. Pop. Biol.* 20, Princeton University Press, Princeton, New Jersey.
- Wrege, P. H., and Emlen, S. T., 1994, Family structure influences mate choice in White-fronted Bee-eaters, *Behav. Ecol. Evol.* 35: 185-193.
- Wunderle, J. M., and Martinez, J. S., 1987, Spatial learning in the nectarivorous bananaquit: Juveniles versus adults, *Anim. Behav.* 35:652-658.
- Wynne, C. D. L., 1995, Reinforcement accounts for transitive inference performance, *Anim. Learn. Behav.* 23:207-217.
- Yoerg, S. I., and Kamil, A. C., 1988, Diet choices of Blue Jays (*Cyanocitta cristata*) as a function of time spent foraging, *J. Comp. Psychol.* 102:230-235.